Revisiting the consequences of cooperative breeding

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Abstract: Thornton McAuliffe (2015) recently questioned the hypothesis that cooperative breeding has a variety of socio-cognitive consequences, invoking both logical and empirical arguments. The cooperative breeding hypothesis (CBH) posits that the immediate tasks associated with extensive allomaternal care require motivational proximate mechanisms, such as increased social tolerance or proactive prosociality which, as a side-effect, also can facilitate performance in socio-cognitive tasks. Eventually, over evolutionary time this constellation may also, under specific conditions, facilitate increases in brain size. Thus, the CBH is not merely a modified version of the social brain hypothesis, as suggested by Thornton McAuliffe, which would posit that a species has to be particularly smart to engage in cooperative breeding. In this reply, we first clarify these conceptual issues and then systematically address their criticism of the empirical evidence. We conclude that the empirical evidence for the CBH is strong in primates, but that future work on lineages other than primates is required to assess its generality.

DOI: https://doi.org/10.1111/jzo.12322

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Short title: Reply to Thornton & McAuliffe (2015)

Abstract

Thornton & McAuliffe (2015) recently questioned the hypothesis that cooperative breeding has a variety of socio-cognitive consequences, invoking both logical and empirical arguments. The cooperative breeding hypothesis posits that the immediate tasks associated with extensive allomaternal care require motivational proximate mechanisms, such as increased social tolerance or proactive prosociality which, as a side effect, also can facilitate performance in socio-cognitive tasks. Eventually, over evolutionary time this constellation may also, under specific conditions, facilitate increases in brain size. Thus, the CBH is not merely a modified version of the social brain hypothesis, as suggested by Thornton & McAuliffe, which would posit that a species has to be particularly smart in order to engage in cooperative breeding. In this reply, we first clarify these conceptual issues and then systematically address their criticism of the empirical evidence. We conclude that the empirical evidence for the CBH is strong in primates, but that future work on lineages other than primates is required to assess its generality.

Keywords

Cooperative breeding hypothesis, prosociality, social tolerance, callitrichid monkeys, anthropomorphism, primates, species comparisons, extensive allomaternal care

Introduction

In a recent issue of this journal, Thornton & McAuliffe (2015), referred to as T&M from here on, questioned both the logic of, and the empirical support for, the hypothesis that cooperative breeding has a variety of socio-cognitive consequences. We welcome this prominent attention to the hypothesis because if it survives testing, the cooperative breeding hypothesis (CBH) will play an important role in explaining why one great ape lineage became so different, and did so quite rapidly, from the other great ape lineages and gave rise to our own species (Hrdy 1999).

According to the CBH, the proximate motivational mechanisms needed to make the cooperative breeding system work smoothly under naturalistic conditions also happen to facilitate cognitive *performance* (though not necessarily intrinsic *ability* per se) in a variety of socio-cognitive tasks (Figure 1). This idea was inspired by the seminal work of Snowdon (2001), and elaborated by Burkart & van Schaik (2010), referred to as B&vS from here on, mainly focussing on primates. In particular, the CBH argues that the presence of social tolerance, proactive prosociality and other motivations (see below) translates into increased performance in socio-cognitive tasks of social learning, information donation and teaching, gaze understanding and cooperative problem solving (Figure 1; see also Burkart 2009; Burkart & van Schaik 2010; Burkart & Finkenwirth 2014). Below, we examine the evidence for these predictions in light of T&M's critique.

Before doing so, it is important to also stress what the CBH does not claim. It does not claim that a species requires particularly powerful cognitive abilities and a correspondingly big brain to engage in cooperative breeding. Rather, the cognitive consequences arise because the available cognitive potential is expressed differently, and in the above-mentioned contexts, more efficiently (e.g. Burkart and Finkenwirth 2014, page 9). Therefore, CBH is not merely a variant

of the social brain hypothesis, as argued by T&M, which would predict that cooperative breeding required distinct cognitive abilities. Hence, we can only agree with T&M's conclusions that "*there is no compelling evidence that these processes are either unique to cooperative breeders or particularly cognitively demanding*" (page 12) or "*that there is little evidence to suggest that cooperative breeding entails distinct cognitive challenges*" (page 13), but want to stress that these conclusions in no way contradict the CBH.

Once a species has been a cooperative breeder for some time, however, the greater efficiency of social learning relative to independent breeders may lead to natural selection on enhanced cognitive ability, and thus bigger brains. We discuss these evolutionary consequences in detail below.

How to test the CBHs predictions?

Most of an organism's traits are affected by multiple selective forces. The CBH is therefore a *ceteris paribus* hypothesis, and to test it (or indeed any other evolutionary hypothesis) one cannot simply compare a random set of cooperative breeders with a random set of other species. The fact that species other than cooperative breeders learn socially, for instance, is on its own uninformative (see T&M, page 16). Rather, systematic comparisons that control for phylogenetic relatedness and as many other factors as possible are required, such as broad comparative analyses or targeted comparisons.

In broad comparative analyses, the aim is to identify to what extent the intensity of allomaternal care[1] predicts variation in a given trait, e.g. proactive prosociality, across a large

[1] Cooperative breeding, where helpers do not breed, is toward the upper end of the allomaternal care continuum (with eusociality at its extreme, see also Isler & van Schaik 2012). Note that this continuous variable allows for powerful comparative analyses also within primates because this taxon shows considerable variation in allomaternal care.

number of species, by controlling for phylogenetic relatedness and other possible confounding factors, such as brain size. Broad comparative analyses require large bodies of comparative data. In their absence, the method of targeted comparisons can be applied (B&vS, see also SI). Here, the performance of particular cooperatively breeding species is compared with that of their closest, independently breeding sister taxa. Within non-human primates, this implies comparing cooperatively breeding callitrichid monkeys with capuchin and squirrel monkeys. B&vS did this by systematically reviewing the literature on cognitive performance in these species. Targeted comparisons are less powerful statistically than broad comparisons, but when a difference is found in one direction, whereas the major confounding factors would predict the opposite direction, they can be highly informative. The major confounding factor when comparing cognitive performance is brain size, and because capuchin and squirrel monkeys have substantially larger brains than callitrichids, the targeted comparison in B&vS is biased against callitrichid monkeys and thus renders this test of the CBH conservative.

Immediate consequences: Proximate mechanisms and performance in socio-cognitive tasks

B&vS predicted that in primates, the motivational changes needed to sustain cooperative breeding would include increased social tolerance, social monitoring in relaxed contexts, and proactive prosociality. These proximate mechanisms, in turn, would facilitate performance in social learning tasks, information donation and teaching, gaze understanding and cooperative problem solving, and also pave the way for richer and more flexible vocal communication. We tested these predictions with broad comparative analyses and targeted comparisons and found they were met. Here we examine these predictions and T&M's criticisms of them.

Proximate mechanisms regulating caretaking behaviours

Social tolerance

T&M (page 15) claim that *"it is not clear whether cooperative breeders are generally more socially tolerant than other animals, as data for systematic comparisons are lacking*". However, Burkart et al. (2014) had made such a systematic comparison and found a strong effect of allomateral care on social tolerance, as well as an effect of pair-bonding, in a set of 24 groups of 15 primate species (Figure 2). Furthermore, in this data set, variation in social tolerance within the callitrichid monkeys was also linked to variation in allomaternal care (Burkart 2015). Importantly, the measure used by Burkart et al. (2014) is correlated with alternative measures of social tolerance (Cronin *et al.* 2013). This work shows that B&vS's prediction is clearly met in primates.

This result may be somewhat surprising given that cooperative breeding systems are often described as despotic, especially where stress-related suppression plays a role in the reproductive failure of subordinates (meerkats: Young *et al.* 2006). When viewed from the perspective of reproductive skew, they are indeed despotic, but the absence of reproduction by many of the group's adults need not be brought about by permanent social stress. In fact, subordinates in cooperative breeders typically show lower, rather than higher stress levels compared to dominants (Creel 2001), and breeders and helpers in callitrichid monkeys show highly tolerant social relationships (Aureli & Schaffner 2006).

Proactive prosociality

Among primates in nature, cooperatively breeding callitrichid monkeys share significantly more food than independently breeding species, and do so in qualitatively different ways: not only do they allow immatures to take their food, they also offer it in a proactive (i.e. spontaneous, unsolicited) way and call them in when they have found a food item (Brown, Almond & van Bergen 2004; Jaeggi, Burkart & van Schaik 2010). For instance, an analysis of over 7000 food sharing events in captive marmosets revealed that during peak provisioning periods, adults share more than half of all pieces of food they possess, and more than one third of these transfers occur proactively; roughly 10% of all shared food items are shared with other adults (Martins & Burkart 2013).

To identify the motivational processes underlying naturalistic prosocial behaviours such as food sharing, experimental studies have been conducted. As also bemoaned by T&M, however, most studies are not comparable (Silk & House 2011). In fact, methodological differences demonstrably affect the results of prosociality studies (Burkart & Rueth 2013). We therefore decided to use the same, cognitively undemanding paradigm and identical procedures to test one of the major predictions of the CBH in 24 groups of 15 primate species: that more allomaternal care correlates with a greater tendency toward proactive prosociality. These data strongly supported the CBH, and none of various alternative hypotheses (Burkart et al. 2014). T&M raise several methodological issues with this study, and are worried by the variation within callitrichids. A detailed response to the methodological issues can be found in the SI, which shows the conclusions are robust. The variability within callitrichid monkeys had us puzzled as well. However, it turns out that the same factor that explains variation in prosociality and

tolerance across primate species, i.e. allomaternal care, is also linked to variation *within* callitrichid monkeys (Burkart 2015).

Cognitive consequences of cooperative breeding?

The studies reviewed above showed that, as predicted, proactive prosociality and social tolerance increase alongside with increasing levels of allomaternal care in primates. But do these proximate motivational mechanisms of allomaternal care also facilitate performance in a variety of socio-cognitive tasks? The literature reviewed in B&vS suggested it does, but a general concern of T&M was that these findings may be a spurious effect of sampling bias: because cooperative breeders would be more tractable as study systems, they would generally perform better on whichever tests one subjects them to. While one may question this assumption, in particular in primates, it produces a simple prediction: we would expect increased performance by cooperative breeders in both social and non-social cognitive tasks. This, however, was not the case: increased performance by callitrichids was strikingly limited to the social domain.

Social learning

It has been recognized for a long time that social tolerance facilitates social learning (Coussi-Korbel & Fragaszy 1995). A straightforward prediction was therefore that species with extensive allomaternal care engage more in social learning, and B&vS found support for this prediction. For instance, Moscovice & Snowdon (2006) report that cotton-top tamarins showed very rapid social learning without receiving food rewards. In contrast to capuchin monkeys, no evidence for aggression or monopolization of the foraging task was found. Likewise, in directly comparable tests, capuchin monkeys did not socially learn to avoid food made unpalatable with pepper

(Visalberghi & Addessi 2000), whereas callitrichids rapidly did so (Snowdon & Boe 2003). In fact, callitrichids who had sampled the food would utter alarm calls at a high rate.

The review of social learning studies by Custance et al. (2002) shows the same pattern. T&M challenge this conclusion, but their alternative measure does not alter the outcome: cooperative breeders were still twice as likely to be successful social learners than expected. Nonetheless, we agree that future surveys should ideally control for major differences in the mechanisms of social learning.

T&M argue we should look at evidence for social learning from the wild. Evidence for social learning in callitrichids in the wild is clearly available, and by no means restricted to parent-offspring contexts (Gunhold, Whiten & Bugnyar 2014; Gunhold *et al.* 2014). However, even though establishing social learning experimentally in the wild is possible (Reader & Biro 2010), not all species are equally amenable to field experiments, producing biases. Moreover, identifying the actual mechanisms involved is notoriously difficult (Kendal et al. 2010). Thus, wild and captive data complement each other: wild data inform us about the incidence and function, whereas captive data remain indispensable to reveal the mechanism.

T&M also argue that other species are capable of social learning, and that many cooperative breeders do not imitate. Again, we never predicted that only cooperative breeders would be able to learn socially, but merely that *ceteris paribus* they are more likely to do so. In fact, Burkart & Finkenwirth (2014, page 8) argued that the currently available evidence "*suggests that the basic underlying mechanisms for social learning, including imitation, are present in many species but applied in species-specific ways*". In primates, we find a bias towards cooperative breeders, with their higher social tolerance and reduced gaze aversion (De Wandelaer & Burkart 2008; Burkart 2009).

Teaching

Another prediction by B&vS was that the readiness to share food may extend to a tendency to share information, and thus to teach. T&M incorrectly assume that we implied the prediction to concern intentional teaching, which we did not. They also conclude that teaching is not found predominantly among cooperative breeders. This is surprising in light of Thornton & Raihani's (2010, page 299) conclusion that *"…to date, the strongest evidence for teaching has been found in cooperatively breeding species"*. T&M now suggest this pattern "*may well reflect their tractability as study systems*". Although this may hold for some lineages, it clearly does not in nonhuman primates, where extensive attempts have been made to identify teaching, in particular in our closest relatives, the independently breeding chimpanzees, with very limited success (Moore 2013, Kline 2015).

Research into the taxonomic distribution of teaching, and thus resolution of this issue, is hampered by debates about its operational definition. All agree, however, that teaching by adults is most likely where individual learning is costly or opportunities to do so are lacking (Kline 2015). Teaching by felid mothers is clearly consistent with this. The same argument also predicts teaching in tool-using great apes, whose immatures take years to learn how to use tools (Meulman, Seed & Mann 2013). Yet, mothers do not teach, even if they could easily scaffold their infants' attempts (Völter, Rossano & Call 2015). In contrast, teaching-like behaviour in callitrichids is increasingly demonstrated (Dell'MourRange & Huber 2009; Rapaport 2011, Chow et al. 2015, Takahashi et al. 2015), including, surprisingly, indications that they may actually perceive knowledge or skill deficits in naïve individuals, implying they show intentional teaching (Humle & Snowdon 2008, Moura, Nunes & Langguth 2010, Martins & Burkart 2013).

Gaze following, cooperative problem-solving, and communication

The CBH was in part inspired by the finding that common marmosets would readily solve perspective-taking tasks (Burkart & Heschl 2007), which had been used as evidence for simple Theory of Mind understanding, and which chimpanzees passed (Hare *et al.* 2000), whereas capuchin monkeys did not (Hare *et al.* 2003). Likewise, in directly comparable cooperative problem solving tasks, callitrichids cooperate at much higher rates (i.e. 97% when both were rewarded, and 76% when only one cooperation partner was) than independently breeding capuchin monkeys (i.e. 76% and 39%, Snowdon & Cronin 2007).

Especially sophisticated among callitrichid monkeys is their vocal communication (Zuberbühler 2011; Snowdon 2001; Snowdon 2013; Borjon & Ghazanfar 2014, Chow et al. 2015; Takahashi et al. 2015), and in fact we predict that the most pervasive differences between cooperative and independent breeders may well be found in communicative contexts (see also Manser et al. 2014). Our literature review (B&vS) suggested that these are systematic patterns, even though the scarcity of sufficiently comparable data from different species made this conclusion preliminary.

What about other lineages?

The CBH, first introduced by Hrdy in 1999, argued that an ape with the life history attributes of *Homo sapiens* (in particular the co-occurrence of prolonged periods of dependency combined with short birth intervals) could not have evolved unless mothers received allomaternal assistance. Subsequent efforts were aimed at identifying whether there was also a cognitive dimension to the CBH, from the perspective of both immatures (Hrdy 2009, 2013) and helpers (Burkart & van Schaik 2010, Burkart et al. 2009). It was thus specifically developed and

elaborated for the primate lineage (see also SI), and accordingly tests have so far focused on this lineage. Nonetheless, whether the CBH also applies to other lineages is a valid question.

Phylogeny matters in two different ways. First, the predictions of the immediate motivational and cognitive consequences of cooperative breeding are directly derived from the specific helping behaviours performed by helpers (see Figure 1). For instance, fish helpers may fan eggs or defend the territory (Taborsky & Limberger 1981), bird helpers may provision offspring or mob predators (Koenig & Dickinson 2004), and primate helpers may carry the young and do some provisioning (Goldizen 1987). Thus, egg fanning is unlikely to require the same proximate motivational mechanisms as food sharing.

Second, phylogeny may affect the consequences for other aspects of behaviour. Thus, a motivational change towards more prosocial attitudes to fellow group members, which is likely a common trait associated with cooperative breeding across lineages, may well produce different effects in a small mammal than in a chimpanzee-like, large-brained animal (Burkart et al. 2009). For instance, if a great ape capable of simple Theory of Mind understanding starts to engage in teaching, it is more likely to also engage in intentional teaching than a species that teaches but has no Theory of Mind abilities (such as ants). This may have been a critical interaction effect in human evolution (Burkart et al. 2009).

The extent to which the predictions of the CBH developed for primates also apply to other lineages may thus critically depend on lineage-specific idiosyncrasies. In B&vS we addressed this issue and showed that elephants and canids show a similar pattern: they perform surprisingly well in socio-cognitive tasks but not in tasks from the non-social, physical domain. But obviously more systematic comparisons are needed, along with detailed theoretical analyses focusing on the interplay between new traits related to cooperative breeding (e.g. proactive

prosociality) and the phylogenetic substrate upon which they were grafted. Nevertheless, some of the patterns identified in primates seem to even hold in phylogenetically remote lineages such as eusocial insects, which offer spectacular cases of prosocial, declarative communication (bee dance: Couvillon 2012), teaching (tandem running ants: Franks & Richerson 2006), social learning (Leadbeater & Chittka 2007), or cognitive performance suggestive of metacognitive abilities (Perry & Barron 2013) . Eusociality, represents an extreme form of cooperative breeding.

The predictions of the CBH regarding delayed evolutionary consequences will arguably be more stable across lineages because they are only indirectly linked to the idiosyncrasies of the cooperative breeding systems and mainly derived from energetic considerations, as detailed in the following section.

Evolutionary consequences

The evolutionary version of the CBH explores whether allomaternal care may also play a role in the evolution of larger brains. The social brain hypothesis (Dunbar & Shultz 2007) is well supported for birds and mammals, but it leaves much of the variation in brain size unexplained, for instance in the form of so called grade-shifts, i.e. where different lineages differ strongly in brain size unrelated to differences in social demands (Holekamp et al. 2015). To understand this variation, it is crucial not only to focus on the benefits of large brains, but also on their costs (van Schaik et al. 2012). B&vS suggested cooperative breeding played a role in brain size evolution because it influences the cost-benefit balance, not because it "*entails distinct socio-cognitive challenges*" (T&M, p. 13).

Big brains consume a large proportion of the energy available to an organism, in particular in immatures. Moreover, this energy needs to be constantly available, because developing brains cannot be starved temporarily without permanent damage. In cooperatively breeding species, this constraint on brain size can be relieved by the energy subsidies to immatures by alloparents, which therefore, all other things being equal, permits the evolution of bigger brains in species with allomaternal care. However, selection may also favour investing the load reduction of mothers receiving allomaternal care into the production of a higher number of offspring, rather than in brainier offspring. The conditions under which one pathway is more likely than the other are summarized under the concepts of 'life history filter' and 'energy filter' (van Schaik, Isler & Burkart 2012; Isler & van Schaik 2014). Empirical support from broad phylogenetic comparisons is available for both pathways: in birds and some mammals, allomaternal care is linked with higher reproductive rates, in particular so in nonhuman primates, and with bigger brains in mammals in general (particularly so in carnivores, but not in nonhuman primates; Isler & van Schaik 2012).

The balance between costs and benefits of larger brains is further modulated by processes related to cultural intelligence. Brains per se do not provide a fitness advantage to individuals, but rather the skills that are learned ontogenetically do. Since social learning is per definition more efficient than individual learning, a brain of the same size will acquire more fitness-relevant skills if it does so via social rather than asocial, individual learning. The cultural intelligence approach thus predicts that species able to rely more systematically on social learning (for whatever reason, cooperative breeding being one among others), are more likely to be able to evolve a bigger brain (van Schaik & Burkart 2011; van Schaik, Isler & Burkart 2012;

see also Burkart in press, for how cooperative breeding, cultural intelligence and life history interact in enabling the evolution of big brains).

Conclusions

In contrast to T&M, we would argue on the basis of current evidence that the support for the cooperative breeding hypothesis is actually surprisingly strong, at least for primates, the lineage in which systematic comparative work has been done. Of course some predictions remain untested. Such tests should ideally be along the lines of Burkart et al. (2014), thus involving, as called for by T&M, *"phylogenetically controlled analyses, accounting for ecological variables such as diet and using cognitive data obtained using comparable methods*". In particular, we hope that T&M's critique will stimulate similar comparative studies in the taxa on which T&M are experts, so we can test the generality of the effects of cooperative breeding on the motivational and cognitive aspects of behaviour. In biology, phylogeny matters, as do all manner of confounding variables, and it is conceivable that effects are to some extent taxon-specific. Mapping these effects in some detail is laborious but unavoidable.

Acknowledgements

We thank Sarah Hrdy, Karin Isler, Michèle Schubiger, and Charles Snowdon for useful comments on a previous draft of this manuscript. This work was supported by the Swiss National Science Foundation (SNF grants 105312-114107 and 310030-13083 to JB).

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Figure Legends

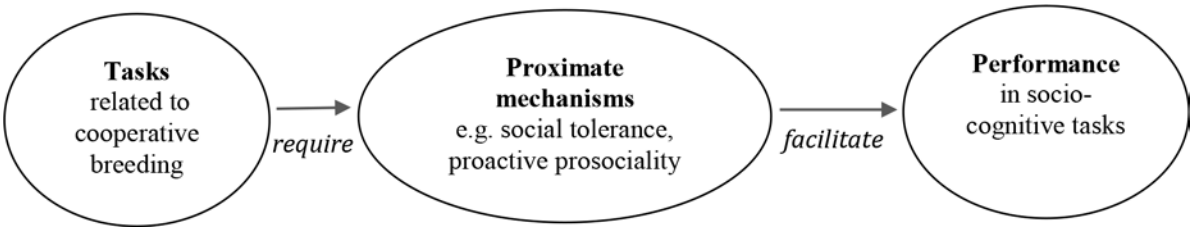

Figure 1

The hypothesized pathway for a link between cooperative breeding and socio-cognitive performance. The CBH predicts that cooperative breeding – or extensive allomaternal care – is associated with a set of proximate mechanisms necessary to support and enable allomaternal behaviors. At the same time, these proximate mechanisms facilitate performance (but not necessarily ability) in a variety of socio-cognitive tasks. For instance, cooperatively breeding primates show increased levels of social tolerance, which is necessary to ensure smooth infant transfers in the canopy At the same time, however, social tolerance also facilitates performance in social learning tasks (see text).

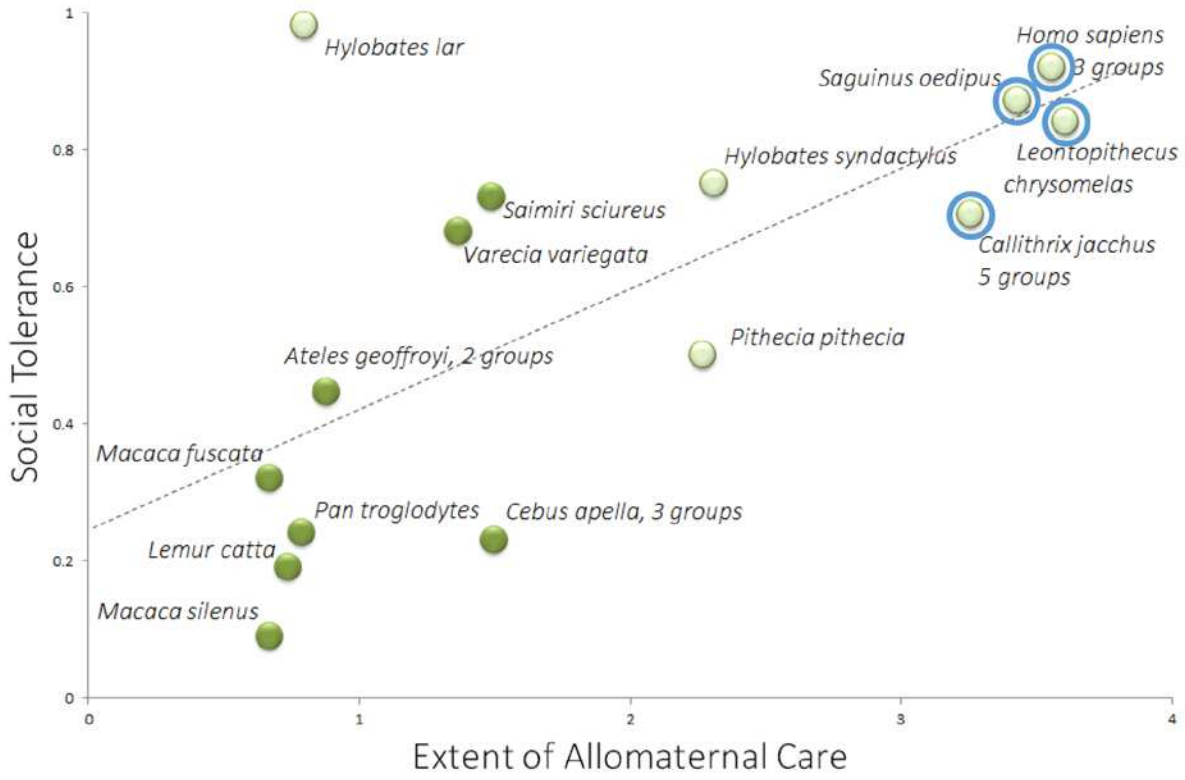

Figure 2

Relationship between allomaternal care and social tolerance in primates. Light green dots: pair bonded species; blue circles: species qualifying as cooperative breeders.

Supplementary Information

1) Targeted comparisons

When broad comparative analyses are not possible to test evolutionary hypotheses, targeted comparisons can be performed, i.e. comparisons between closely related sister taxa that differ with regard to the relevant factor but are as similar as possible with regard to potential confounding factors. The necessity to focus on targeted comparisons in closely related species, rather than comparing any species that differ with regard to the relevant factor is depicted in Figure 2. This figure exemplifies how the comparison of randomly chosen species, one an independent breeder and one a cooperative breeder, may result in the independent breeder outperforming the cooperative breeder even if in reality, the trait in question is indeed positively linked with cooperative breeding. It is thus important to keep in mind that the comparison of any two randomly chosen species, one breeding cooperatively but the other one breeding independently, has no explanatory power for the CBH if we cannot exclude other factors that may also affect the trait of interest.

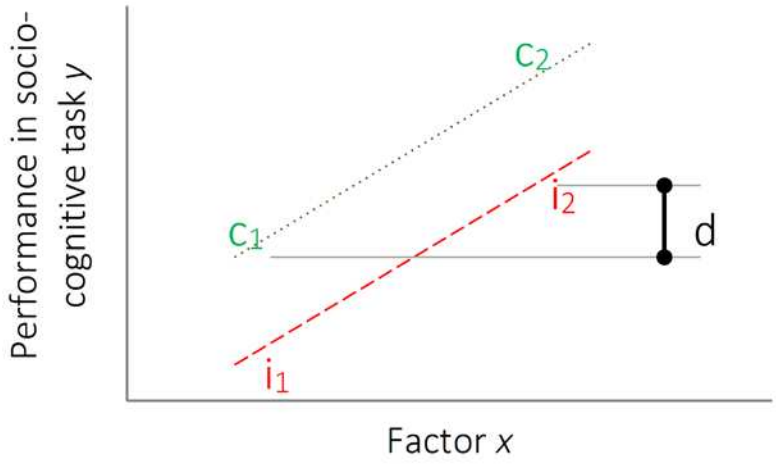

Figure 2
Schematic depiction of a situation where cooperative breeding has a positive influence on cognitive performance (green dotted regression lines: cooperative breeders; red dashed line: independent breeders; c_1 = cooperatively breeding species 1, i_1 = independently breeding sister taxon of c_1; etc.). Targeted comparisons show that in each species pair, the cooperatively breeding species outperforms its sister taxon. However, if additional factors also play a role (factor x, e.g. brain size), comparing non-sister taxa that vary widely with regard to this factor is uninformative or may even wrongly lead to the opposite conclusion (because i_2 outperforms c_1 by distance d).

1

2) Methodological issues of the group service study (Burkart et al. 2014)

In the group service paradigm, which had been designed to provide a comparable measure of proactive prosociality across species, one animal can pull food toward the group but cannot get any of it for itself. The apparatus is very simple and prior to the test, the animals have to demonstrate they understand it; during the test, several control conditions are included to make sure they continue to do so. The paradigm had been piloted with three species and found to be robust (Burkart & van Schaik 2013). The subsequent comparative study, involving 24 groups of 15 different primate species, found strong support for the CBH, and none for a range of other hypotheses. Thornton & McAuliffe (2015) raise three issues with the group service, (i) that it is limited to primates only, (ii) that there is substantial variation within callitrichids, and (iii) methodological issues. While (ii) has been addressed empirically (Burkart et al. 2015) as well as in the main text, (i) and (iii) are discussed below.

Re (i): Main focus on primates and anthropocentrism

T&M criticize our approach as anthropocentric. In one sense, we accept this criticism. The aim of evolutionary anthropology is to try and understand why humans became so different from the other great apes. We hypothesise that extensive allomaternal care was partly, perhaps even largely responsible for this. In other words, we assume that a non-unique process, convergently found in other lineages, has had predictable effects in our own lineage. Our main comparative effort focused on primates for this reason as well. In fact, the CBH developed by Hrdy in 1999 was that an ape with the life history attributes of *Homo sapiens* (in particular the co-occurrence of prolonged periods of dependency combined with short birth intervals) could not have evolved unless mothers had allomaternal assistance. Subsequent efforts were aimed at identifying whether there was also a cognitive dimension to the CBH, both from the perspective of helpers (Burkart & van Schaik 2010, Burkart et al. 2009) and of immatures (Hrdy 2009, 2013). Neither version requires actors involved to be particularly brainy to start with.

The charge of anthropocentrism is not accurate when read in the sense that we project human abilities onto the animals or are only interested in those features that have direct human equivalents. We apply the comparative method and aim to understand the evolution of our own species as one would try to understand the evolution of any other species using this approach. Moreover, primates are not a bad lineage in which to examine the consequences of allomaternal

care because they show quite pronounced variation in this feature, in fact much more so than any other mammal lineage (see Figure 1 in Isler & van Schaik 2012).

Re (iii): Methodological issues

T&M are concerned that some results were artificially produced by order effects because the experiment was run in phases. In phase III of the experiment, we trained all individuals to understand the apparatus, i.e. they had to be able to pull the handle with one hand, and simultaneously take a piece of food with the second hand, in a position as remote as possible so that they would still be able to just reach the food when completely extending their arms. They thus learned that the board would pull back automatically if it was released, and had to pass predefined criteria to proceed to the next phase. In phase IV of the experiment, in which we assessed prosociality, we ran 5 test sessions and 5 control sessions on alternating days, each consisting of a total of 70 trials. In test sessions, the board was baited with a piece of food in a position which made it impossible for an individual to pull the handle and retrieve the food by itself at the same time. Food could only be made available to the group if one individual would pull the board and another would retrieve the food. In control sessions, the board was not baited but the empty food bowl was audibly manipulated, to control for the possibility that individuals would pull for reasons other than providing food. Only individuals who pulled more in test vs. control sessions were included in the analyses. Furthermore, T&M wrongly criticized that we hadn't used difference scores as dependent variables, but in fact we had done so (Burkart et al. 2014, Supplementary Information, page 22), but this did not affect the conclusion. Finally, in both test and control sessions, so called motivation trials were interspersed, identical to phase III, where food could be made available individually. In the motivation trials, food items were virtually always taken, which clearly demonstrates that over test session, the subjects had not forgotten how the apparatus worked.

For those species that had shown consistent provisioning over all test sessions in phase IV, we had added an additional control condition in phase V to exclude further alternatives for high levels of provisioning. Phase V was identical to phase IV, but access to the food in the more distant position was always blocked (but still available in motivation trials). T&M argued that the animals pulled less in phase V, not because they understood that they could no longer provide food, but because of a general decline in pulling over the experiment. If this argument

were correct, the conclusion that increased allomaternal care elicits increased proactive prosociality would no longer be compelling.

There are at least two lines of evidence against the interpretation suggested by T&M. First, supplementary Figure 3 in Burkart et al. (2014) clearly shows that species with high levels of allomaternal care do not reduce their pulling activity over the time of the experiment. Over the test sessions in phase IV, we found three clusters. The first contained groups with provisioning rates that were low throughout, the second contained groups with decreasing rates, and the third groups with stable high or increasing rates of provisioning. Tellingly, species from the first cluster had the lowest level of allomaternal care, the second cluster slightly higher, and the third cluster had the highest levels of allomaternal care. It was this third group of species that had been subjected to the final phase V, to provide additional evidence that they indeed understood the consequences of their pulling (which is obviously not possible for species who do not pull for others in the first place), and they passed this phase. Second, for two callitrichid groups we re-ran phase IV tests after the end of the experiment, with the result that they immediately resumed pulling for their group members at similar rates as before (Burkart et al. 2014, Supplementary Information, page 15). In the meantime, additional callitrichid groups have been tested again with phase IV trials for various reasons, and they also immediately resumed to pull for each other (unpublished data). In fact, we now use the group service apparatus as an environmental enrichment device for the callitrichid groups at our primate station, and it is possible to provide entire meals via these devices. The published finding is therefore robust.

Lest this conclusion be misinterpreted, we stress that prosocial behaviour may be heterogeneous in terms of its motivating factors (Jaeggi, Burkart & van Schaik 2010). Hence, these results do not mean, as implied by T&M, that species without extensive allomaternal care do not show prosocial behaviour. They do, but it is more commonly solicited by the proximity and behaviour of a special friend or relative. Moreover, we do not exclude other sources of proactive prosociality, e.g. between particular highly bonded dyads, in other species, but so far there is no clear evidence that that occurs. Again, the hypothesis is a *ceteris paribus* one, like virtually all ideas in biology.

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